

SEROTINY AND CONE-HABIT VARIATION IN
POPULATIONS OF *PINUS COULTERI* (PINACEAE) IN
THE SOUTHERN COAST RANGES OF CALIFORNIA

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ABSTRACT

The cone habit of *Pinus coulteri* exhibits considerable variation among plant communities in the southern Coast Ranges of California. Serotiny is prevalent in *P. coulteri*/chaparral, *P. coulteri*/*Quercus chrysolepis*, and *P. coulteri*/*Cupressus sargentii* communities that are periodically burned by wildfire. The bulk of pine regeneration in these types occurs in the first year after a fire, after which it rapidly declines, and ceases within 20 years. By contrast, in the *P. coulteri*/*Q. agrifolia* community nearly all cones open at maturity or soon thereafter. Pines in this habitat are generally less subjected to fire-caused mortality; regeneration, although sporadic, is continuous.

The quantity of stored viable seed is reduced in all community types by animal depredations and varying degrees of spontaneous cone opening. Despite these losses, the amount of stored, viable seed retained in serotinous stands is 50 times greater than quantities stored in nonserotinous stands.

Three closely related species of the genus *Pinus*, *P. torreyana*, *P. sabiniana*, and *P. coulteri*, constituting the subsection *Sabinianae*, show tendencies toward seed retention (McMaster and Zedler 1981; Critchfield, pers. comm.). *Pinus torreyana* retains seed for up to 15 years in cones that open gradually over time (McMaster and Zedler 1981). Minnich (1980) suggested that the often abundant regeneration of *P. coulteri* following wildfire originates from seed stored in partially open cones and maturing cones persistent on fire-killed trees. Despite these tendencies, however, serotiny, defined as the retention of mature seeds in closed cones, is not known to occur in this group.

In this study I describe serotiny, cone-habit variation in relation to plant community types, and factors that influence seed retention in *P. coulteri* growing in the southern Santa Lucia and La Panza Ranges, part of the southern Coast Ranges of California. I also discuss the possible adaptive value of canopy-stored seed in fire-prone habitats and management implications of seed storage and other life history traits of *P. coulteri*.

THE STUDY AREA

The study area includes a highly fragmented *P. coulteri* distribution in part of the Los Padres National Forest (Fig. 1). The tree ranges in elevation between 610 m and 1525 m, and average annual

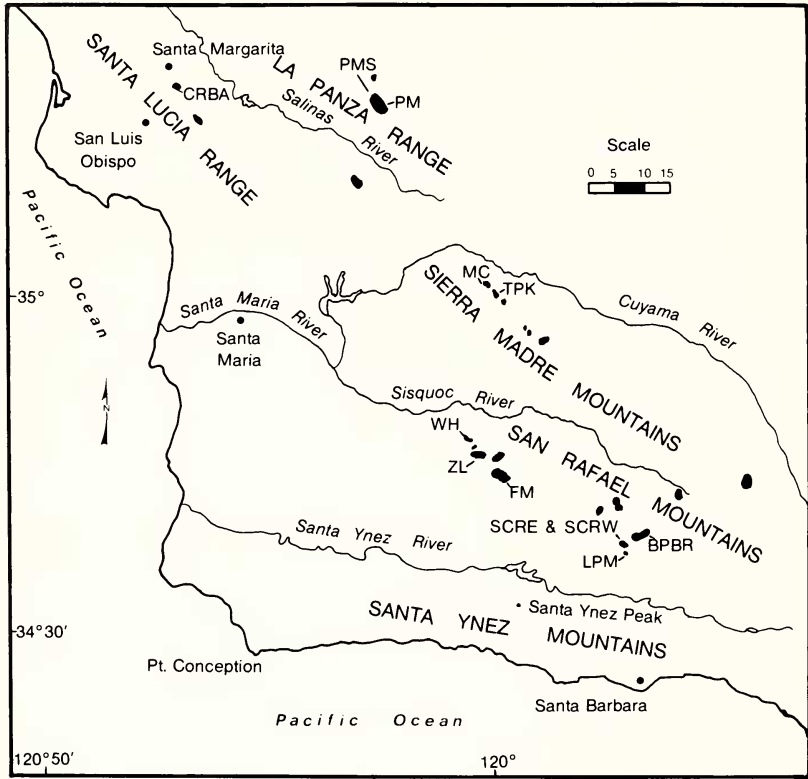


FIG. 1. The distribution of *Pinus coulteri* and the location of sampling sites in the study area.

precipitation generally exceeds 450 mm. Stands grow on a variety of soil types (Table 1), but gravelly loams derived from marine bedrock parent material are the most common.

The climate of the region is Mediterranean. At lowland localities like Santa Barbara (36 m) and San Luis Obispo (60 m), most precipitation falls from November–April. Mean monthly precipitation and temperature range from 30–100 mm and 11–15°C, respectively. May–October is dry and warm: mean monthly precipitation and temperature for this period vary from 0.5–10 mm and 16–20°C, respectively. Data from Santa Ynez Peak (1310 m) and Figueroa Mountain (FM; 960 m) (Fig. 1) indicate that precipitation at higher elevations extends into May and ranges from 30–186 mm for the six month period.

Wildfires are very frequent in the region. Since 1912, major fires (>4000 ha) have burned on the average of once every three years,

TABLE 1. LOCATION AND HABITAT DETAILS OF *P. coulteri* SAMPLE SITES IN THE STUDY AREA. Key: D, density in no. plants/ha; and, BA, basal area in m²/ha.

Sample site	Elevation, aspect, slope, soil family	<i>Pinus coulteri</i>		Other tree species	D	BA	Shrub cover %
		D	BA				
Big Pine-Buckhorn Road (BPBR)	1438 m, se., 5-40% Supan	45	1.3				70
Cuesta Ridge Botanical Area (CRBA)	806 m, n., 50% Cuesta-Henneke	239	8.2	<i>Cupressus sargentii</i>	1458	50.0	2
Figueroa Mountain (FM)	1244 m, se., 60% Witzel-Skalan	154	0.5	<i>Q. agrifolia</i>	60	2.9	
Little Pine Mountain (LPM)	1341 m, sw., 35% Witzel	148	20.0	<i>Q. agrifolia</i>	46	2.2	25
Miranda Canyon (MC)	1304 m, nnw., 64% Morical and Konocti	900	29.0	<i>Q. chrysolepis</i>	208	8.1	
Pine Mountain (PM)	975 m, wsw., 45% Supan	936	0.1				77
Pine Mountain Summit (PMS)	1137 m, e., 50% Supan	242	31.4				96
Santa Cruz Road East (SCRE)	1335 m, e., 35% Witzel	72	1.6				98
Santa Cruz Road West (SCRW)	1335 m, w., 60% Witzel	2754	0.2				15
Timber Peak (TPK)	1448 m, nnw., 65% Morical and Konocti	307	20.0	<i>Q. chrysolepis</i>	320	11.9	
Wildhorse (WH)	945 m, nw., 50% Witzel	230	11.6	<i>Q. agrifolia</i>	141	4.6	
Zaca Lake (ZL)	729 m, ene., 5-20% Witzel-Skalan	68	6.5	<i>Q. agrifolia</i>	65	50.6	22

and most (60%) spread through chaparral older than 40 years. Because 52% of the vegetation is currently older than 40 years, large-scale conflagrations are inevitable in future dry seasons (U.S. Forest Service data on file at the Supervisor's Office, Goleta).

Chaparral, semidesert chaparral, and coastal sage scrub collectively cover 73% of the study area, followed by 5% oak woodland and 3% conifer forest. Three *P. coulteri* communities are common in the study area: *P. coulteri*/chaparral, *P. coulteri*/*Quercus agrifolia* and *P. coulteri*/*Q. chrysolepis*. Fifty-five percent of *P. coulteri* forests occur with chaparral. This community occupies a variety of exposures on slopes ranging from 5–81%. *Adenostoma fasciculatum* and *Arctostaphylos glandulosa* are the most common understory species, although richer mixtures of brush species are encountered on more mesic sites. Shrub cover usually exceeds 70%, but is often lower in dense pine stands, or where soils are thin on outcroppings.

Pinus coulteri/*Q. agrifolia* forest is the next most common community (23%), and occurs mostly on gentler slopes (<50%), southerly exposures (Campbell 1980) and ridgetops. Exotic annual (*Bromus* spp., *Festuca* spp., and *Avena* spp.) and indigenous perennial grasses (*Bromus carinatus* and *Elymus glaucus*) dominate the understory with several subshrubs in *Lupinus* spp. Shrub cover is less than 30%.

Pinus coulteri/*Q. chrysolepis* forest (20%) is confined almost entirely to steep (>60%) north-facing aspects. *Toxicodendron diversilobum* is the only common understory species, but its cover is low (Campbell 1980). The *P. coulteri*/*C. sargentii* forest grows at a single locality in the area (CRBA) (Fig. 1).

STUDY METHODS

Twelve stands were sampled from most parts of the *P. coulteri* distribution in the study area (Fig. 1). The stands were selected subjectively to represent a variety of community types of differing ages. Each stand had to be native (i.e., unplanted), relatively accessible, undisturbed, and homogeneous in vegetation. It is estimated that at least 50% of the major *P. coulteri* stands are represented. The CRBA stand is anomalous because it straddled a sheltered fuel-break. However, there were no signs of pine cutting in this stand, although *C. sargentii* was thinned.

Elevation, slope angle, and aspect were recorded at each site. Soil classification was taken from a third order soils map (U.S. Forest Service data on file on file at the Supervisor's Office, Goleta). Depending on the size and density of the stand, tree density was estimated with circular plots or by the plotless point-center-quarter method (Cottam and Curtis 1956). Small (<0.75 ha) or relatively dense stands were sampled with plots varying in size from 0.05–0.2 ha. Each plot was made large enough to include 30–60 pines ≥ 2.5

cm in diameter measured at 1.4 m (dbh). Larger sample sizes were necessary to characterize multi-aged stands. In low-density stands larger than one hectare (SCRE, ZL), the point-center-quarter method was employed. In each stand a total of 12–15 points was sampled along 2–3 transects oriented parallel to the contours. Tree density estimates using this method had standard errors less than 10% of their mean values.

All *P. coulteri* seedlings (≤ 2.5 cm dbh), saplings (2.5 cm–10 cm dbh) and trees (> 10 cm dbh) were counted in plots and at sampling points on the transects. Fewer than 5 seedlings were encountered in each of the WH, ZL, and LPM stands. Stems ≥ 5 cm were cored at 60 cm to determine age. In addition, two to four stems were cut at ground level in several stands to estimate the number of years required to reach 60 cm; as a result, four years were added to the core-height age of trees in all stands. No attempt was made to estimate the mean and variance in the age required to reach 60 cm in each stand. All other tree species ≥ 2.5 cm dbh were counted and measured.

Shrub cover was visually estimated in 2.3 m² circular subplots taken at each sampling point along transects or at 8–15 locations within the plots. Total herbaceous cover also was recorded for each subplot and the dominant species noted.

Open and closed cones were censused and aged with binoculars. Since over 95% of cones in 15- to 50-year trees are borne on the bole, cone age can be determined indirectly by counting the number of branch whorls. Generally, trees in this age class produce whorls annually. Nevertheless, in order to verify the accuracy of whorl counts, one to two branches were cut from a sample of 5–15 trees per site, and the branch ages compared to their corresponding whorl counts. The two were highly correlated ($r = 0.948$, $p < 0.01$, $n = 14$, SCRW; $r = 0.974$, $p < 0.01$, $n = 31$, SCRE; $r = 0.947$, $p < 0.01$, $n = 19$, CRBA).

Branch cones in trees older than 50 years could not be aged accurately using binoculars because branch growth had slowed enough to prevent distinction between recent cones, which remain closed during the normal maturation period, and those that remained closed longer. Accurate aging could only have been accomplished by counting bud-scale scars, which would have required tree felling or branch cutting. Thus, only the number of open and closed cones was recorded in these trees. All stand samples had at least 10 trees 15–50 years old.

To simplify analysis of cone age data, cones were grouped into one-year age class intervals. Thus, cones 0–12 months are in the first age class, 13–24 months in the second, and so on. Cone production is assumed to have commenced on 1 June, when pollination first was observed in the SCR and PM stands.

A total of 251 closed cones, varying in age from 16 months to 24 years, was gathered from trees in PM and SCRE stands: 156 cones from 26 trees in the SCRE stand, and 95 cones from 25 trees in the PM stand. Cones were selected from trees that appeared visually to have an adequate number of cones in certain size classes. Cones remaining closed for more than two years after pollination are termed serotinous in this study. Each cone was first measured and examined for external signs of animal damage, and then immersed in boiling water for 60–75 seconds to melt the resinous bonding material that seals the scales together. Once the scales had separated, the seeds were hand-extracted. In addition, residual seeds were removed from 28 open cones (5–17 years) gathered from the SCRE stand. Empty seeds were removed by floating in water.

Germination trials were conducted on a random sample of 20 filled seeds from each cone. Because of the small number of filled seeds in each open cone, they were combined into one lot from which three samples were tested. After soaking in an aerated water bath for 24 hours, each sample was dipped in a captan solution and sown on a moist layer of cotton in a petri dish. Following a stratification period of 60 days at 10°C in continuous light, the light-temperature regime of the samples was altered to 8 hours of light at 25°C and 16 hours of darkness at 15°C. A seed was considered germinated if it produced a radicle at least 3 mm long after 14 days. The small sample size of cones in some age classes required the grouping of germination results for analysis.

A description of cone maturation was constructed from small samples of cones (4–10 at each sample age) collected 12, 14, 16, 18, and 22 months after pollination (1 June) in the LPM and SCRE stands, and 16-month cones in the PM stand.

RESULTS

Age structure and establishment. Stand age data indicate two general types of age structures: unimodal, bell-shaped distributions indicative of even-aged stands, and pulsed distributions suggesting irregular episodes of successful regeneration (Figs. 2–3).

Most *P. coulteri* stands growing in association with chaparral (SCRE, SCRW, PM), *Q. chrysolepis* (MC, TPK), or *C. sargentii* (CRBA) are characterized by an even-aged structure that results from a stand-killing wildfire. Evidence corroborating this explanation is provided by Minnich (1978, 1980), who noted high levels of fire-caused pine mortality in both *P. coulteri*/chaparral (90%) and *P. coulteri*/*Q. chrysolepis* (81%) types in the eastern Transverse Ranges. Comparable pine losses probably occur in *C. sargentii* thickets, which are prone to crown fires (Vogl et al. 1977).

The PMS stand is anomalous. It is an old-aged pine stand in

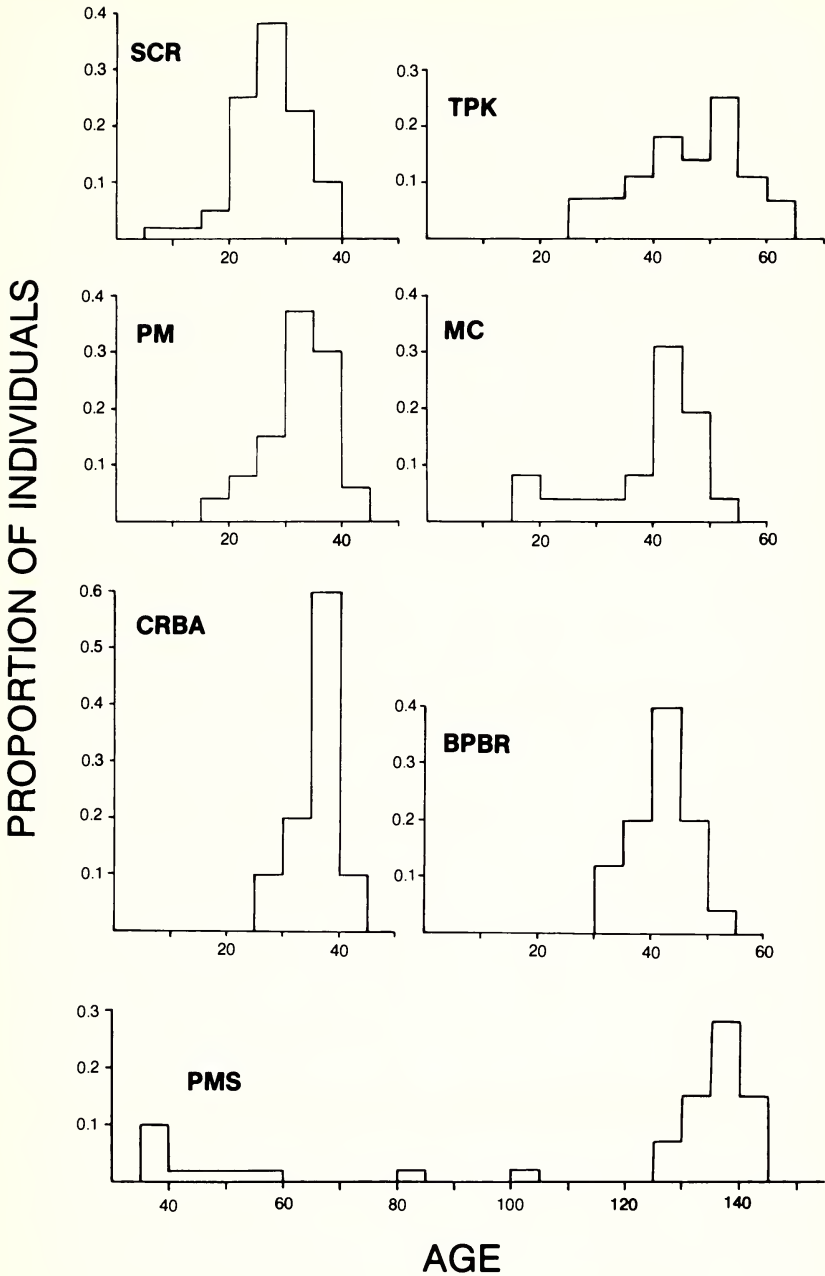


FIG. 2. Age-frequency histograms for the *P. coulteri*/chaparral (BPBR, PM, PMS, and SCR); *P. coulteri*/*Q. chrysolepis* (MC, TPK); and *P. coulteri*/*C. sargentii* (CRBA) stands. The SCRE and SCW are nearly identical and have been combined into SCR.

chaparral with several episodes of pine establishment. The oldest cohort likely originated after a fire in the 1830s. Another documented fire swept the area in 1921, but evidently spared most of the 90-year-old trees. Fire scar analyses of 140-year-old trees indicate that a fire that burned an adjacent area in 1939 also spread to the PMS site. The isolated 80- and 100-year-old trees suggest that chaparral stands relatively well-protected from stand-converting fires may exhibit pulsed regeneration at an advanced age. In a discussion of 40-year-old, south-slope, montane chaparral of the type often associated with *P. coulteri*, Hanes (1971) noted the formation of openings in the canopy resulting from shrub mortality. These openings were colonized by *Salvia mellifera* seedlings. Similarly, *P. coulteri* seedlings may establish in these sites. My observations of canopy openings in comparatively young stands (<60 years), however, suggest that such establishment is probably rare and most likely occurs on the periphery of the stand.

Complete or nearly complete stand destruction is followed within a year by a burst of pine regeneration (Minnich 1977, Griffin 1982). Seeds fall from heat-opened, maturing cones, residual seed in open cones, and older closed cones stored in the canopy. Age-frequency histograms (Fig. 2) show the appearance of new trees consistently later than the first year after the fire. To a large extent, this discrepancy can be attributed to the variable growth period necessary for seedlings to reach the core height. In dense stands, for example, numerous seedlings do not reach 60 cm even after 6 years (Griffin, pers. comm.). Inadequate precipitation and poor site conditions may also retard seedling growth.

As vegetative cover increases with stand age, tree establishment declines and eventually ceases. Despite the variety of species associated with *P. coulteri* among the even-aged stands, the length of establishment, as determined by the age difference between the oldest and youngest trees in each stand, was remarkably constant, averaging 23 ± 1.86 years ($n = 7$). The actual establishment period is probably around 20 years, since very late appearing trees would likely require more time to reach the core height. Vale (1979) found that successful regeneration of *P. coulteri* in a chaparral stand on Mt. Diablo spanned 19 years.

Although first-year seedlings originate from fire-released, cone-stored seed, later pine regeneration probably developed from other sources. These include: (a) occasional trees that survived fires. Some trees, especially those on ridgetops, are undamaged by fire and continue to supply seed to burned areas for decades. Such survivors were present in both the SCR and TPK stands; (b) singed, but unopened cones on fire-killed trees. After a recent fire (1981) in a *P. coulteri*/*Q. agrifolia* stand, some large, heavily scorched pines had unburned or lightly singed cones on the tips of high branches. Con-

TABLE 2. CONE AND SEED CHARACTERISTICS OF THE PM AND SCRE STANDS. All attributes are significantly different ($p < 0.05$, one-way ANOVA) between the two stands, except full seeds/undamaged cone. Cone size is length \times maximum width. Means are presented \pm one standard error.

Cone and seed characteristics	Study site			
	PM	n	SCRE	n
Cone size	209.3 \pm 4.2	133	159.0 \pm 5.3	44
Seed length (cm)	1.43 \pm 0.02	75	1.26 \pm 0.03	75
Seed weight (gm)	0.35 \pm 0.01	2420	0.29 \pm 0.01	1780
Full seeds/undamaged closed cone	150.5 \pm 5.6	111	151.3 \pm 5.9	88
Percent empty seeds/closed cone	15.7 \pm 1.3	134	9.8 \pm 1.1	82
Full seeds/open cone	2.2 \pm 0.4	28	no data	

ceivably, these cones might open slowly enough to furnish viable seed to the area for several years after the fire; (c) early reproducing trees of the immediate post-burn cohort. Reproduction can occur in trees as young as 10 years (Minnich 1980). Seed released from precociously reproducing trees appeared to be the likely source of trees where no obvious survivors were observed (PM, CRBA, MC); and (d) residual seed trapped in the basal scales of open cones (Table 2).

Irregular pulses of pine regeneration characterize the *P. coulteri*/*Q. agrifolia* stands (Fig. 3). Some even-aged cohorts date back to fires, whereas others probably coincide with years of good precipitation and seed production. Typically, small groups of pine seedlings appear in grassy openings or at the edge of the oak canopy. Saplings are often spindly, and some heavily shaded individuals die. Nevertheless, many manage to reach a fire-resistant size. Because ground fuels in this habitat consist of grasses and discontinuous patches of shrubs and subshrubs, wildfires are generally lower in intensity, and crown fires are probably rare. For example, fire-caused pine mortality averaged only 30% in a similar *P. coulteri*/*Q. kelloggii* type in the eastern Transverse Ranges (Minnich 1977). Both forests are open, free of brush and *Q. chrysolepis*.

Age of first reproduction. Based on the age of the oldest serotinous cones in the SCRE and PM stands, as well as observations of saplings at other locations, reproduction in most *P. coulteri* begins 12–15 years after germination. Published figures range from 8–20 years (Krugman and Jenkinson 1974) to 15–20 years (Minnich 1980). High tree density may significantly delay reproduction. Thus, although the two SCR stands are the same age, reproduction in the extremely dense SCRW stand began five years after the adjacent low-density SCRE stand. Late-establishing trees often grow poorly because of

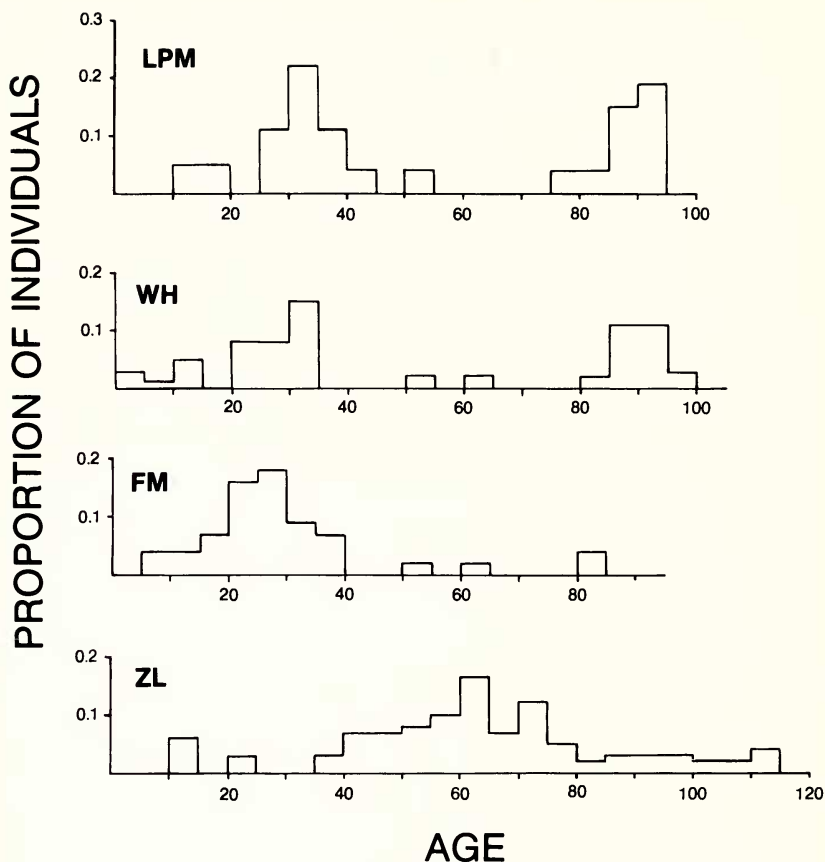


FIG. 3. Age-frequency histograms for the *P. coulteri*/*Q. agrifolia* stands.

brush competition or suppression by overstory trees. Thus, cones are infrequently encountered in trees of reproductive age.

Trunk and branch cone production. Young trees typically bear whorls of up to four cones (rarely five) on the bole. Cones do not appear at the ends of branches until limbs are strong enough to support the heavy cones (the heaviest in the Pinaceae). The age of first branch-cone production differed markedly among stands. Trees in the low-density, fast-growing SCRE stand produced branch cones 20–25 years after germination, whereas cones occurred in small numbers on 36- to 40-year-old trees in the considerably denser CRBA, PM, TPK and MC stands. Limb cones were not produced in the extremely dense SCRW stand. As the stand ages, cone production shifts almost entirely to tips of the major branches and apex of the crown (Minnich 1980). It is not uncommon, however, to find

tiers of serotinous cones dating back 20 years on the trunks of trees as old as 50 years.

Cone maturation. Twelve-month (June) cones are similar in size to mature cones. However, 12-month cones are green, firm, and pulpy compared to mature cones, which are hard, brittle, and light caramel in color. Seeds at this stage are full-sized, but white and soft, lacking any trace of a hard seed coat.

By 14 months (August), the umbos of outward-facing scales begin to turn dark brown. Cones are typically moist, but the scales are fibrous and separate individually when heated. The seed coat is hard and light brown instead of black. Only 11% of the seeds were solid; of these, 50% were viable. Cones burned at this stage of ripening probably contribute only marginally to pine regeneration.

Most cones turned to mature-cone color after 16 months, although some retain a reddish hue. Seeds are fully formed and, despite the somewhat milky texture of the endosperm, have a high germination rate (Table 3).

By 18 months (December), cones have completely matured, and judging by the degree of cone development at 16 months, most probably reach full maturity between 15 (September) and 16 months (October) after pollination.

Cone weathering. Serotinous cones retain a light-caramel color for 2–3 years. Almost invariably by the fifth year, however, outward-facing scales show signs of weathering as the apophyses begin to gray. In succeeding years the signs of weathering spread, and the abundant resinous covering of newly-ripened cones gradually wears away. Fifteen-year cones are almost entirely gray and usually devoid of external resin. Cones reaching 24–26 years are heavily weathered, usually to the point of disintegrating. This weathering sequence conforms closely to that described for *Pinus banksiana* cones (Roe 1963).

Cone and seed characteristics. Table 2 summarizes cone and seed characteristics of the PM and SCRE stands. Cone size, seed length and weight, and the percent empty seeds per cone differ significantly between the two populations. Despite these differences, however, the mean number of full seeds per undamaged cone is similar in the two stands.

Seed viability. The viability of seeds from closed cones of all ages from the SCRE and PM stands is high, 83–100%, and shows no decline with cone age. This trend contrasts with similar studies of other serotinous pines, *P. clausa* (Cooper et al. 1959), *P. banksiana* (Schantz-Hansen 1941, Beaufait 1960) and *P. pungens* (Barden 1979), in which seed viability decreases with cone age. High viability appears to be related to protection afforded by the tightly sealed scales that cover the seed with a hard, woody layer 1–1.5 cm thick. High

TABLE 3. CONE-HABIT CHARACTERISTICS AND STORED VIABLE SEED ESTIMATES FOR THE TWO *P. coulteri* PLANT COMMUNITY GROUPS. STORED viable seed estimates assume 138 solid seeds/cone and 91% viability. Open cones are assumed to have 2.2 solid seeds/cone and 97% viability.

Study site	Open cones/tree	Closed cones/tree	% open cones	Viable seeds/tree	Stored viable seeds/ha
<i>Q. agrifolia</i> stands					
FM	0.23	0.30	43.4	38.2	5878
LPM	0.73	0.35	67.5	45.5	6735
WH	0.02	0.10	16.7	12.6	2898
ZL	0.77	0.45	63.1	58.2	3954
$\bar{x} \pm S.E.$	0.44 ± 0.18	0.30 ± 0.07	47.7 ± 11.6	38.6 ± 9.6	4866 ± 876
Chaparral, <i>Q. chrysolepis</i> , and <i>C. sargentii</i> stands					
BPBR	0.64	7.64	7.7	960.8	43,236
CRBA	0.00	5.71	0.0	717.1	210,100
MC	0.16	2.37	5.4	678.1	610,319
PM	0.06	4.29	1.4	538.8	504,371
PMS	0.13	14.20	0.9	1783.5	431,610
SCORE	1.29	8.60	13.0	1082.7	77,957
SCRW	0.06	0.18	25.0	22.7	62,605
TPK	0.00	3.14	0.0	394.3	121,057
$\bar{x} \pm S.E.$	0.29 ± 0.16	5.77 ± 1.55	6.7 ± 3.1	772.3 ± 185	$257,657 \pm 79,377$

seed viability (97%) from open cones suggests that the seed coat may also provide additional protection, although it was not possible to determine how long seeds in open cones were exposed at the time of collection.

Insect damage to cones. In early stages of development (<16 months), cones are highly susceptible to insect attack. For example, 71% of the SCRE cones in the 2–4-year age classes were infested by *Dioryctria auranticella* (ponderosa pine coneworm). Damage was complete in 25% of the collected cones. However, in the 5–7-year age classes partially damaged cones decreased to 36%, 11%, and 9%. Insect damage was absent in cones older than 7 years. Directly or indirectly, insect infestations caused an average loss of 67 full seeds per attacked cone, or a 45% reduction. Seed losses may have been elevated further by the mining of *Camponotes anthrax* (carpenter ants), a frequent inhabitant of damaged cones.

Complete cone losses to insects in the PM stand were far less frequent than in the SCRE stand (<1%). Insect-damaged cones in 2–9-year age classes varied from 25–40%, whereas cones older than 9 years showed no signs of recent insect attack. Altogether, there was a reduction of 57 full seeds per damaged cone, or a 38% seed loss. Nearly all the cones in the PM collection were infested by larvae of *Chrysophana canocola* (flatheaded cone borer). Although this species is not known to attack pine seeds (Essig 1958), its extensive tunneling may weaken the cone's resistance to weathering.

The diminishing percentage of insect-attacked cones in increasingly older age classes indicates that damaged cones probably weather, disintegrate and fall before unattacked cones. However, there was no evidence to suggest that insect tunneling caused serotinous cones to open or encouraged squirrel consumption.

Variation in serotiny. The degree of serotiny differed markedly among the *P. coulteri*/chaparral, *P. coulteri*/*Q. chrysolepis*, *P. coulteri*/*C. sargentii* stands (Fig. 4). The highest degree of serotiny was exhibited by the PM stand; fully 52% of the cones 6 years or older were closed. By contrast, none of the MC cones was closed after 4 years. Between these extremes the other stands form a gradient, but exhibit no discernible pattern of variation.

Attempts to assess serotiny in the *P. coulteri*/*Q. agrifolia* stands were only partially successful. Trees younger than 50 years were present in all the stands and were particularly abundant in the WH and FM stands. These stands were notable for their scarcity of cones in comparison to the even-aged stands regardless of tree age (Table 3). The small cone populations suggest that either (a) they opened at maturity and were blown from the trees, or (b) they remained closed at maturity but were cut by *Sciurus griseus anthonyi* (western gray squirrels) before they could age further.

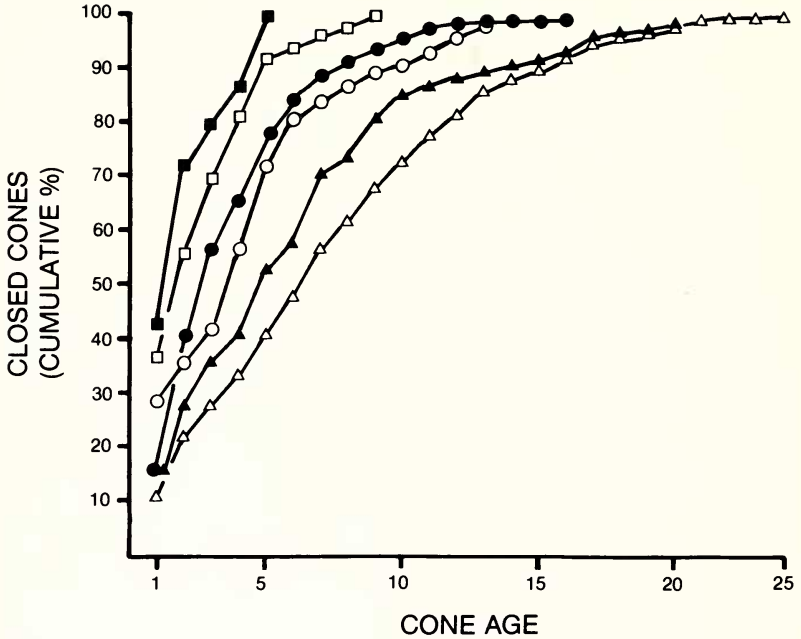


FIG. 4. Cumulative cone-age distributions for the serotinous BPBR (▲), CRBA (○), MC (■), PM (△), SCR (●), and TPK (□) stands. The SCRE and SCRW stands have identical distributions displayed as SCR.

Several lines of evidence point to cone opening at maturity. Few trees in the age class 15–50 years with an adequate sample of attached cones had closed cones older than 2 years. On the periphery of the LPM and FM stands in chaparral, pines appeared less prone to squirrel depredations than those in the central portion of the stand, judging by the numerous attached cones in the older age classes (4–6). Significantly, nearly all the cones in these outlying trees were open. And finally, the percentage of open cones/trees in these stands was nearly 8 times ($p < 0.01$; one-way ANOVA, arcsine transformation) that of the even-aged stands (Table 3).

There are at least three factors that clearly influence the length of time that cones stay closed and attached to the tree: (a) insect damage, (b) cone cutting by squirrels, and (c) spontaneous cone opening. As discussed previously, insect-attacked cones disappear from the cone population before undamaged cones. Because coneworm infestations are generally widespread, insect damage probably has a significant but highly variable effect on cone persistence.

Squirrel cone cutting and consumption was observed in all stands.

Both green and mature cones were cut and consumed on the ground, or less frequently, partially consumed while attached to the tree bole or limbs. Scales of some cones were partially or entirely stripped from the main axis while others appeared to be excavated with only the half shell remaining.

Western gray squirrels are known to depend heavily on acorns and pine seeds for winter food supplies (Stienecker and Browning 1970, Stienecker 1977). Evidence for this dependence was readily observed in the *P. coulteri*/*Q. agrifolia* habitat. For example, a random sample of 125 ground cones in the ZL stand showed that 44% had signs of squirrel damage, including removal of basal scales, partial excavation, or complete scale removal. Seventy-five percent of a sample of 108 cones on the ground in the FM stand were squirrel-damaged. In most the scales had been stripped completely from the cone axis. Observations suggest that *P. coulteri* cones are a relatively dependable year-round food source for squirrels. Moreover, squirrel population density and stability may be closely tied to cone production by this pine in southern California, a relationship perhaps comparable to that of serotinous *P. contorta* and squirrels of the genus *Tamiasciurus* in the Cascade Mountains of Washington (Smith 1970).

Spontaneous cone opening occurred in varying degrees in nearly all stands (Table 3). Perry and Lotan (1977) cited three factors explaining differential cone opening: differences in scale tension, environmental effects on bonding strength, and genetic differences in the bonding oleoresin. In a study of *P. contorta*, they found opening differences between new and old serotinous cones from the same tree, suggesting that melting characteristics of the resin seal may be influenced by the environment. A complex interaction of genetic and environmental factors probably determines cone opening in *P. coulteri*, but differentiating between the two will require further study.

Stored viable seed. Table 3 gives estimates of stored viable seed for sampled stands. The number and viability of seeds in open and closed cones in the *Q. agrifolia* stands are assumed to be the same as the chaparral stands. A comparison of seed populations between the two community groups reveals a marked difference. Although there is considerable within-group, interstand variability, the *P. coulteri*/chaparral, *P. coulteri*/*Q. chrysolepis*, *P. coulteri*/*C. sargentii* stands taken together average 50 times the number of stored viable seeds in the *P. coulteri*/*Q. agrifolia* stands ($p < 0.01$; one-way ANOVA, logarithmic transformation). I attribute most of this between-group difference to the higher incidence of both squirrel cone cutting and spontaneous cone opening (i.e., less serotiny) in the *P. coulteri*/*Q. agrifolia* stands.

DISCUSSION

There is a discernible pattern of cone-habit variation among sample stands in the study area. The open-cone habit predominates in the *P. coulteri*/*Q. agrifolia* forest, where fire-caused mortality is low and pine regeneration relatively unrestricted by competing vegetation. Serotiny tends to be well developed in communities subject to killing crown fires. Previous studies (Minnich 1977, Griffin 1982) indicate that pine establishment in fire-prone communities is relatively synchronous, peaking in the first post-fire year. Thereafter, establishment declines and eventually ceases within 20 years as competing vegetation gradually dominates the site.

Habitat-related cone-habit variation similar to that described above has been recorded for a number of pine species (Little and Dorman 1952; Lotan 1967, 1968; Givnish 1981). Indeed, several investigators have proposed that serotiny has evolved in direct response to fire (Perry and Lotan 1979, Givnish 1981, McMaster and Zedler 1981). Extensive evidence linking fire frequency and serotiny was presented for *P. rigida* in the Pine Barrens of New Jersey (Givnish 1981). Similarly, results of this study suggest that cone-habit variation in *P. coulteri* is strongly influenced by fire. Indeed, the pattern of variation corresponds favorably to that predicted by a model for the evolution of serotiny in Mediterranean-climate conifers proposed by McMaster and Zedler (1981). They argue that serotiny is selected for when: (a) stand-killing fires burn over extensive areas, (b) interfire intervals are too short for reproduction by second-generation trees, and (c) fire size is too large for seed dispersal from adjacent unburned areas to be a significant factor for recolonization of burned areas. As discussed previously, stand-immolating fires are common in the *P. coulteri*/chaparral, *P. coulteri*/*Q. chrysolepis* and *P. coulteri*/*C. sargentii* communities, and average fire size is usually large relative to the seed dispersal abilities of *P. coulteri*. The average fire-free interval, however, is often long enough (Byrne 1979) to permit some reproduction by second generation trees. Thus, limited seed release is favored, as was observed in even the most serotinous stands.

When any of the above conditions are sufficiently relaxed, open-cone behavior is favored. Hence, the generally low fire intensity in *P. coulteri*/*Q. agrifolia* forests assures that open-cone trees can leave offspring that survive and reproduce. Closed-cone behavior, on the other hand, is not favored in this fire regime because seed-releasing crown fires are infrequent.

The retention of substantial quantities of viable seed has obvious adaptive value to fire-killed pine stands that regenerate in the face of heavy post-burn tree and chaparral competition. The accumulation of seed in serotinous cones insures that the maximum number

of seed is available to take advantage of a transient post-burn environment conducive to seedling growth. In addition, cone-stored seed acts to buffer year-to-year fluctuations in seed production (McMaster and Zedler 1981). If stand regeneration were dependent entirely on seed in ripening cones, a crown fire coincident with a poor cone year could severely curtail stand replacement. Serotinous cones guarantee that at least some seed will fall after the fire.

An abundant seed rain may also be crucial to pine reestablishment in habitats with a limited supply of microsites sufficient for seed germination and seedling growth. In this regard, Wilson and Vogl (1965) noted locales in the Santa Ana Mountains where successful *P. coulteri* establishment was confined to rivulets, channels, and eroded areas. The dissemination of large numbers of propagules may enhance the chances of seed encounter with these "safe sites" (Harper et al. 1965).

Finally, serotiny may confer superior competitive status to *P. coulteri* in mixed conifer stands burned by recurrent fire. In at least one stand in the Santa Lucia Mountains, Griffin (1982) recorded a very high post-burn *P. coulteri*/*P. lambertiana* seedling-to-tree ratio (6.65) compared to the prefire ratio (0.15). He attributed this inversion of relative species abundances in part to the release of stored seed by *P. coulteri*. Lotan (1976) cites the serotinous cone habit as a major reason for the aggressive reinvasion of disturbed sites by *P. contorta* at the expense of other conifers.

Understanding the variation in cone habit as well as other life history traits of *P. coulteri* is vital to the management of this species. In southern California fire suppression activities have created extensive tracts of old, highly flammable vegetation subject to catastrophic fires (Minnich 1983). In recent years, land management agencies have introduced prescribed burning as a means of creating a less flammable vegetation mosaic of younger age classes. This means that *P. coulteri* in its various habitats will be managed increasingly under controlled burn conditions (Dougherty and Riggan 1981).

Burn objectives, of course, vary depending on the desired outcome whether it be complete or partial stand regeneration. When the goal is complete stand turnover, knowing whether there is adequate stored seed for natural regeneration is essential (Lotan 1976). Another consideration is timing the burn so that it coincides with maximum viability of seeds in maturing cones. The limited data presented here suggest that ripening seed would not contribute measurably to pine regeneration until after mid-September. Obviously, the quantity of stored viable seed is but one factor affecting the post-burn abundance of *P. coulteri*. Others include fire intensity, precipitation, and post-fire competition.

One aspect of seed retention not adequately investigated in this

study is the relationship between canopy storage of seed and stand age. In many serotinous species stored viable seed increases with stand age (Roe 1963, Vogl 1973, Zedler 1981). In this study, the sample size of stands of differing age growing in similar environmental settings is too small to observe clear trends. My general impression from field observations, however, is that stored viable seed decreases rather than increases with stand age. In older trees, most cones are bunched at the crown apex or grow singly at the ends of branches. Branch-cone production tends to be spotty, and closed cones seldom accumulate well back on the limbs in the same way they do on the trunks of young trees. Additionally, there appears to be more active cone cutting in older stands, perhaps because large old trees furnish an abundance of denning sites resulting in higher squirrel densities.

If net seed accumulation diminishes with stand age, then it may become increasingly difficult to secure natural pine regeneration by prescribed burning. Further, trees in excess of 100 years appeared especially susceptible to insect and disease attack as well as to wind breakage. Consequently, excessive periods of protection from fire may be detrimental to stand persistence.

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ANNOUNCEMENT

ASPT HERBARIUM TRAVEL AWARDS

The American Society of Plant Taxonomists is pleased to announce the availability of competitive awards for travel by graduate students to the nation's herbaria. The awards will not exceed \$500 and will be used to help pay expenses to and from any herbarium (or herbaria) in the United States and per diem expenses during the visit. Competitions for awards will be held twice a year. The first competition deadline is 1 January 1985, with the second deadline 1 July 1985. The grants program will last a minimum of three years (six competitions). Interested Master's or Ph.D. graduate students should send a curriculum vitae, two letters of recommendation (including one from the major professor), a two or three page outline of the proposed research emphasizing the role that the visit to the herbarium will play, and a letter from the Head Curator, Chairman or Director of the institution(s) to be visited indicating willingness to receive the visitor. Awards will be announced by 1 March from the January competition and during the annual banquet of the ASPT from the July competition. Students are encouraged to obtain additional funds from their home institutions (or elsewhere) to extend their research visits even further. This competition is open to students of both cryptogamic and phanerogamic groups. Completed applications and additional questions should be directed to TOD F. STUESSY, Chairman, ASPT Committee for Systematics Collections, Department of Botany, Ohio State University, 1735 Neil Avenue, Columbus, OH 43210. (Phone: (614) 422-5200 or (614) 422-8952.)

BERKELEY HERBARIUM

Severe space limitations require that the Herbarium of the University of California, Berkeley (UC) box and store all vascular plant specimens originating from Europe, Africa, Asia, and the Pacific Basin. Specimens from these areas will be unavailable for loan or routine consultation. However, special arrangement can be made to see them. Please write to the Director of the Herbarium to arrange to use these collections. Collections from North and South America remain unaffected; exchange programs will also remain unaffected. We regret the inconvenience that the inaccessibility of these collections may cause researchers and will try to resolve our space problems so that Eastern Hemisphere specimens will be available again as soon as possible. UC has acquired additional space to house these collections and hopes to obtain storage cases within the next year. For the next decade, the collection at UC will be housed in two locations within close proximity. As the University of California completes the renovation that began this year of all biological science facilities, the collections of the University Herbarium will be brought together in a single expanded and modernized facility.—THOMAS DUNCAN, Director—UC and JEPS.